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A REVISION OF THE VERNAL SPECIES OF
HELENIIUM (COMPOSITAE)

HOWARD F. L. ROCK

(Continued from page 116)

The author has deliberately refrained from referring to the vernal species of *Helenium* throughout the earlier portion of this paper in any formal subgeneric sense in order to make his position clear at this point. Ordinarily, the vernal species of *Helenium* conform to at least a subgenus in *Helenium*, if one were to follow the concepts that prevail in the *Compositae* today. However, inasmuch as this revision was conducted primarily on the basis of herbarium specimens and the data they provide, and to a lesser extent on field studies, any change in the formal subgeneric classification of *Helenium* from that

which prevails in the *Synoptical Flora* and *Die Natürlichen Pflanzenfamilien* does not seem warranted at this time. Until data can be accumulated from sources other than those used up to the present and judged in relation to similar kinds of data for the other portions of the genus *Helenium*, the conservative expedient of maintaining the subgeneric *status quo* seems advisable. Therefore, following Gray and Hoffmann for the present, the various morphological species-groups that exist in *Helenium* are recognized here as Sections.

Provided below is a synopsis of the sections of *Helenium* and those genera allied to it, the GALARDIAE of Nuttall:

SYNOPSIS OF THE SECTIONS OF HELENIUM AND ALLIED GENERA

- A. Receptacle appendaged; the appendages being either in the form of indurated subulate setae, occurring in the interstices between the achenes or else as pentagonal or hexagonal indurated cupules surrounding the achenes, but in neither case paleaceous in form.
 - B. Appendages setiform.....*Gaillardia*.
 - B. Appendages cupuliform.
 - C. Pappus scales lanceolate to elliptic-lanceolate in outline, the apices acute.....*Balduina*.
 - C. Pappus scales suborbicular to reniform in outline, the apices obtuse.....*Actinospermum*.
- A. Receptacle naked, i.e. without definite appendages, the surface denticulate at the most.
 - D. Style branches appendaged; the filiform and hispidulous appendage extending from the penicillate portion of the style branch which terminates the stigmatic portion.....*Gaillardia*.
 - D. Style branches unappendaged, the apices truncate and penicillate.
 - E. Cauline leaf bases (at least those of the midcauline leaves) decurrent along the stem forming wings on the stem.
 - F. Pubescence of the involucre red-black
Helenium Section HECUBAEA
 - F. Pubescence of the involucre colorless to tawny or involucre glabrous.
 - G. Ray florets lacking.
 - H. Plants perennial with a short, fibrous-rooted caudex; perennation by leafy offsets; disk color red-brown; central Florida and eastern Texas
Helenium flexuosum (Section LEPTOPODA).

- H. Plants annual-biennial with a coarse tap-root; leafy offsets usually absent; disk red-brown, rose-purple, blue-purple or yellow.
- I. Plants of western Texas, Mexico, Arizona and Baja California Sur
Helenium Section TETRODUS.
- I. Plants of coastal southern California and Baja California del Norte *Helenium* Section HELENIUM.
- G. Ray florets present.
 - J. Ray florets neutral, their achenes abortive *Helenium* Section LEPTOPODA.
 - J. Ray florets styliferous, their achenes fertile, though slow-maturing.
 - K. Plants annual-biennials, usually with numerous heads on short peduncles and the heads relatively small; disk florets predominantly quadrimerous *Helenium* Section TETRODUS.
 - K. Plants perennial, heads relatively large and on elongate peduncles; disk florets predominantly pentamerous *Helenium* Section HELENIUM.
- E. Cauline leaf bases not decurrent along the stem and the stem not winged.
 - L. Inner involucral bracts distinctly scarious and pappus-like, in contrast to the foliaceous outer bracts; disk corolla lobes glabrous; achenes with gross, corky, densely hispid ribs; dried plants with a *Melilotus*-like odor *Amblyolepis*. (Section AMBLYOLEPIS in Hoffmann)
 - L. Inner involucral bracts not markedly different in quality from the outer bracts; disk corolla lobes glandular-pubescent; ribs of the achenes not distinctly gross or corky in relation to the body-proper of the achene; dried plants without a *Melilotus*-like odor.
 - M. Ray corollas oblong to barely oblong-cuneate in shape, usually many times longer than wide; outer involucral bracts not distinctly reflexed at maturity, often becoming indurated at the base with maturity; inner involucral bracts equal to or exceeding the outer series, or if the inner series is subequal to the outer series, then the involucral base tomentose

Helenium Section OXYLEPIS. *Hymenoxys*
(incl. *Tetraneuris*, *Rydbergia*, *Actinella*, *MacDougalia*)

- M. Ray corollas distinctly and broadly deltoid-cuneate; involucre bracts decidedly reflexed at maturity; the inner series of involucre bracts shorter than the outer series and the involucre base not tomentose. *Helenium* Section HELENIUM. (*Helenium amarum*¹ and *Helenium badium*)

INFRASECTIONAL RELATIONSHIPS

MORPHOLOGICAL CONSIDERATIONS

The six species of the Section LEPTOPODA may be easily placed into two categories on the basis of external form and aspect, and the shape of the pappus scales. These two subgroups and the species included in them are:

- A. Monocephalous; unbranched; yellow disk color; pappus elliptic-lanceolate to elliptic-ob lanceolate, obtuse and unawned.

1. *Helenium pinnatifidum*
2. *Helenium vernale*
3. *Helenium Drummondii*

- B. Oligo- or polycephalous; branched; red-brown disk color; pappus obovate to suborbicular, obtuse and unawned or else lanceolate-acuminate and awned.

¹ There is no doubt in the author's mind that the plant designated by Rafinesque as *Galardia amara* (Fl. Ludov. 69. 1817) is identical to Nuttall's later *Helenium tenuifolium* (Jour. Acad. Sci. Phil. 7: 66. 1834.) Rafinesque's description is quoted below:

217. *Galardia amara* Raf. Caule apice paniculate, ramis unifloris, foliis linearibus reflexis glabris, ligulis apice dilatatis tridentatis Raf.—*Anthemis* Robin p. 440. This plant has not the habit of *Anthemis*, but rather of a *Galardia*; as Robin describes it imperfectly, it may, however, be either, or even an *Helenium*. Stem rising about one foot and a half, round and smooth, with many long leaves of deep green. Perianth [involucre] small embricated with unequal leafy folioles, rays much longer, phoranth [receptacle] spherical (seeds perhaps naked). The whole plant is odoriferous and intensely bitter, it gives an abominable bitter taste to the milk of the cows that feed on it in summer, when the plant thrives and keeps green notwithstanding the greatest drought. It grows at Atakapas [Mississippi] near roads and houses but was brought there accidentally.

Therefore, the following new combination is proposed to reinstate the prior specific epithet proposed by Rafinesque:

Helenium amarum (Raf.) H. Rock comb. nov.

Galardia amara Raf. Fl. Ludov. 69. 1817.

Helenium tenuifolium Nutt. Jour. Acad. Sci. Phil. 7: 66. 1834.

NEOTYPE: Collected by C. R. Ball, no. 182, 6 Sept. 1898 at Alexandria, Rapides Parish, Louisiana (US-364605).

4. *Helenium brevifolium*
5. *Helenium campestre*
6. *Helenium flexuosum*.

On the basis of the above characters and a series of characters that have been judged to have a "primitive" or "advanced" standing within the genus *Helenium* listed below, a scheme reflecting the evolution that has occurred within and between these two subgroups seems possible. The term "subgroup" is used here only for purposes of discussion. It is not used as a formal taxonomic category within the section LEPTOPODA.

PRIMITIVE	ADVANCED
1. Perennial habit	1. Annual-biennial habit
2. Vernal flowering	2. Aestival or autumnal flowering
3. Leaves non-decurrent	3. Leaves decurrent
4. Monocephalous, unbranched	4. Polycephalous, branched
5. Heads large, long-pedunculate	5. Heads small, short-pedunculate
6. Involucral bracts short, broad, numerous, non-reflexed	6. Involucral bracts long, narrow, fewer, reflexed
7. Receptacle broad, convex	7. Receptacle narrow, conical
8. Heads radiate, rays styliiferous	8. Heads discoid or rays neutral
9. Rays homochromatic and yellow	9. Rays heterochromatic, yellow and/or red
10. Disk yellow	10. Disk red-brown, rose-purple or blue-purple
11. Disk florets pentamerous	11. Disk florets quadrimerous
12. Pappus present, more than 5-membered, scales large, awnless, more or less entire-margined	12. Pappus absent or pappus 5-membered, scales reduced in size, awned, margin more or less distinctly modified
13. Achenes pubescent	13. Achenes glabrous
14. Distribution restricted, plants of mesic habitats	14. Distribution wide-spread, plants of varied habitats, increasingly more xeric
15. Plants of coastal, humid, southerly areas	15. Plants of upland, drier, northerly areas

Helenium pinnatifidum is considered to be the least specialized or the most primitive species within the section LEPTOPODA. In addition to the characters given for the first subgroup (which is interpreted as the more primitive subgroup), two leaf characters exhibited by *H. pinnatifidum* are interpreted as being primitive within the section. First, only the mid-cauline leaves are decurrent along the stem, with the wings so formed not exceeding

5 mm. in extent. Secondly, the radical leaves of *H. pinnatifidum* do not taper so as to form a petioloid structure, but instead, are inserted on the stem within the rosette without a pronounced basal constriction.

Along with these leaf characters, *H. pinnatifidum* has decidedly pubescent peduncles and involucral bases. Moreover, the achenes are hairy-pubescent. These characters of pubescence are interpreted as ancestral to the glabrous condition of the peduncles, involucral bases and achenes encountered in one of the other species of the section LEPTOPODA. The smaller size of the pappus scales of *H. pinnatifidum* is in direct contrast, however, to the presumed primitive and ancestral position of *H. pinnatifidum*, a large size and a more foliaceous nature of the pappus scale being considered a primitive character. However, it has become axiomatic that the characteristics of a taxon may or may not be all at the same phyletic level, *i. e.* all advanced or all primitive. The evolutionary position of some characters of a taxon may be more advanced in relation to the remaining characters of the taxon and those of other taxa.

Helenium vernale is considered to occupy a more advanced phyletic position than *H. pinnatifidum*. This advanced position is confirmed in part by the rather complete decurrency of all but the uppermost *cauline* leaves to such an extent that the stem is more or less winged from node to node, in contrast to the restricted type of decurrency exhibited by *H. pinnatifidum*. The ultimate advancement of this character is met with in *H. flexuosum* and most of the other non-vernal decurrent-leaved species of *Helenium*, where even the bract-like leaves subtending the peduncles are noticeably decurrent.

In *H. vernale* the radical leaves are petioloid in form, being rather sharply contracted toward the leaf base to form a petiole-like structure before re-expanding within the rosette so as to become somewhat sheathing at the place of insertion. Again, this character is encountered in the other vernal species with the exception of *H. campestre* and *H. flexuosum*.

The peduncles and involucral bases of *H. vernale* are glabrous, or occasionally glabrescent. In any case, the achenes of *H. vernale* are always glabrous, and this taxon is the only vernal *Helenium* that has glabrous achenes. It would appear that

H. vernale has been derived from *H. pinnatifidum*, the smaller size of the pappus scales of *H. pinnatifidum* being considered a secondary reduction in that species after the derivation of *H. vernale*.

Helenium Drummondii seems to occupy a phyletic position nearly on a par with *H. vernale*, though some of its morphological characteristics would place it as an intermediate between *H. pinnatifidum* and *H. vernale*. The leaf characters of *H. Drummondii* are like those of *H. vernale*. The size of the pappus scales, though larger than those of *H. vernale*, is more in accord with them than with those of *H. pinnatifidum*. However, the pubescent achenes, pubescent peduncles and lanulose involucre bases of *H. Drummondii* indicate an affinity to *H. pinnatifidum*.

The pappus scales of *H. Drummondii* are distinctively slashed into a multitude of *fimbriae* with the *fimbriae* forming more than half the body of the pappus scale and are crimped or crinkled at maturity. The unique pappus scale of *H. Drummondii* represents the only known case of a real elaboration of the pappus scale in the genus *Helenium*. True, many species of *Helenium* possess awned pappus scales but these are regarded as a morphological form correlated with a reduction of the pappus scale rather than as an elaboration of the pappus scale. A final character is that the length of the rays in *H. Drummondii* is usually longer than the length of the rays in the other two taxa of this first subgroup. Such a character may be evaluated as a feature indicating a primitive nature. However, while large rays are usually considered as a primitive character of the *Compositae*, they could possibly also be due, in this case, to a secondary enlargement of the ray, once styliferous, but now neutral. Because of the retention of presumed primitive features, but with the incorporation of several advanced ones, *H. Drummondii* is perhaps best regarded as having had a common derivation with *H. vernale* from *H. pinnatifidum*, but subsequently the two taxa, *H. vernale* and *H. Drummondii*, have had an independent development.

Helenium brevifolium, in the second subgroup, is much like *H. vernale* and *H. Drummondii* in the characters associated with the leaves, both cauline and radical. The cauline leaves are noticeably decurrent and the radical leaves are petioloid. Whereas the basal leaves in the first subgroup are elliptic- to oblong-

linear-lanceolate in outline, the basal leaves of *H. brevifolium* are more oblanceolate to obovate. The few heads are borne in a corymb-like manner, with the long peduncles more or less equal. The peduncles and involucre bases are lanulose, with the pubescence of the involucre base being tomentose at times. The heads are more hemispherical or subglobose than the broad and more or less plane heads of the first subgroup. The disk color is red-brown, with a tendency, however, in some plants to become sordid yellow under certain ecological conditions. The pappus scales of *H. brevifolium* are equivalent in size to those of *H. pinnatifidum* but they differ in form and outline. In *H. brevifolium* the pappus scales are obovate in outline and are more or less distinctly clawed at the base. There appears to be no adequate reason for supposing *H. brevifolium* to have been derived from any member of the first subgroup except through the indirect evidence of the incorporation of the advanced features of the branched habit, multi-headedness and the red-brown disk color.

Helenium campestre appears to have a relationship to both *H. brevifolium* and *H. flexuosum*, much like that of *H. Drummondii* to *H. vernale* and *H. pinnatifidum*. *Helenium campestre* resembles *H. brevifolium* in many of its vegetative and habit characters. However, the ray florets have a tendency to be longer and the pappus scales are the most reduced ones encountered in the vernal species. The pappus scales are only 0.5 mm. long, subobovate to suborbicular in outline and are not clawed. The achenes, moreover, unlike any others in the vernal species, are puberulent rather than hairy-pubescent. In this respect, both in the pappus scales and achene pubescence, *H. campestre* shows a morphological similarity to the annual-biennial species (Section TETRODUS) of Texas and Mexico. On the other hand, *H. campestre*, like *H. flexuosum*, does not have petioloid radical leaves, but rather, the radical leaves are like those of *H. pinnatifidum* and the species of *Helenium* outside of the Section LEPTOPODA. In addition, both *H. campestre* and *H. flexuosum* have pubescent stems and leaves, a character not encountered in the otherwise glabrous-stemmed and glabrous-leaved species of the Section LEPTOPODA.

Helenium flexuosum is quite anomalous in many respects, as far as the other species of this section are concerned. How-

ever, its distribution, neutral and sterile ray florets and perennial nature indicate that it technically belongs to the Section LEPTOPODA. The following features of *H. flexuosum* are aberrant within this neutral-rayed section:

1. The 4-merous condition of the disk corollas, both lobes and stamens
2. The persistent and frequent rayless condition of some specimens from Texas and Florida
3. The bicolor to completely red-colored rays of some Texan and Arkansan specimens
4. The pappus of only five scales, awned and more or less costate for the most part, though occasionally unawned but with acuminate apices
5. The paniculate type of branching
6. The numerous small heads with few broadly deltoid rays
7. The conical receptacle
8. The extended flowering period, ranging from March through November.

These characters, along with the pubescent stems and leaves, and the non-petioid radical leaves, are much more characteristic of the annual-biennial species (Section TETRODUS) of *Helenium*. In fact, the vegetative similarity of *H. flexuosum* to these annual-biennials of Texas and Mexico is such that, if all the heads were removed, *H. flexuosum* would most likely be taken for one of these annual-biennials, were it not for the perennial caudex.

In addition to these morphological characters, the distribution of *H. flexuosum* seems unusual in relation to that of the other species of this vernal section. The Section LEPTOPODA can be characterized, with the exception of *H. flexuosum*, as plants of a relatively restricted kind of habitat and distribution. These species occur in quite moist locations in the Coastal Plain or bogs of the Piedmont of the southeastern United States. Not one can be regarded as a dominant or even conspicuous element in the flora of this region. M. L. Fernald, though, has aptly termed *H. flexuosum* as a plastic and aggressively weedy plant. It inhabits roadsides, old fields, pine barrens, savannahs, hardwoods and low woods from the Coastal Plain to the Appalachian highlands and is encountered from Texas to Illinois, Florida and Maine.

On the basis of this morphological anomaly and ecological diversity it is suggested that *H. flexuosum* is probably of hybrid origin, long-standing in time, and is now a vigorous and quali-

fied weed. The parentage of this presumed hybrid can only be surmised. A most likely candidate for one of the parents is obviously a species of the Section TETRODUS, probably the plant known as *Helenium elegans*. The other parent would logically be one of the vernal species, either *H. brevifolium* or *H. campestre*. However, the greater morphological similarity of *H. campestre* to *H. flexuosum* indicates that it is the more plausible choice. Moreover, the proximity of *H. campestre* to the range of the annual-biennials is an added consideration. In fact, the morphological similarity of *H. campestre* to *H. flexuosum* and the annual-biennials on one side and the morphological alliance of *H. campestre* to *H. brevifolium* on the other suggests that it may not only be the vernal parent involved in this presumed hybrid combination but that it also exhibits possible introgressed characters of the annual-biennials. It must be stated that despite the presumed hybrid origin of *H. flexuosum* and the relationships suggested above, there is no indication that this hybrid process has occurred more than once. There is no indication, either, of subsequent rehybridizations between *H. flexuosum* and either *H. brevifolium* or *H. campestre*. Possibly some of the variation encountered in *H. flexuosum* where its range is sympatric with or abuts that of the annual-biennial species may be attributable to subsequent hybridizations between these two.

It has been possible to postulate a phylogenetic scheme of development for the species of the Section LEPTOPODA on the basis of morphological characters. This scheme results in a division of the species into two subgroups by using a variety of characters related to the external form and aspect of the plants, for the greater part. By utilizing leaf morphology, pubescence and floral characters, an arrangement of the species within these subgroups has been made, as well as speculations concerning their origin and derivation.

There appears to be no decisive reason for considering the second subgroup as having been derived directly from any member of the first subgroup, except through the fact that the second subgroup is more advanced in its morphological features. This lack of an apparent "ancestor" in the first subgroup for the second subgroup suggests that both subgroups may be more or less independent phyletic lines within the section

LEPTOPODA. This leads to the assumption that the divergent tendencies which led to the ultimate formation of these two subgroups may well have been developed (or segregated) soon after or concomitant with the establishment of the tendency that has culminated in the section LEPTOPODA. Presumably, the origin of the section LEPTOPODA has been from some styliiferous-rayed member of *Helenium* or pre-*Helenium* stock. Figure 7 is a diagrammatic scheme presenting these phyletic speculations.

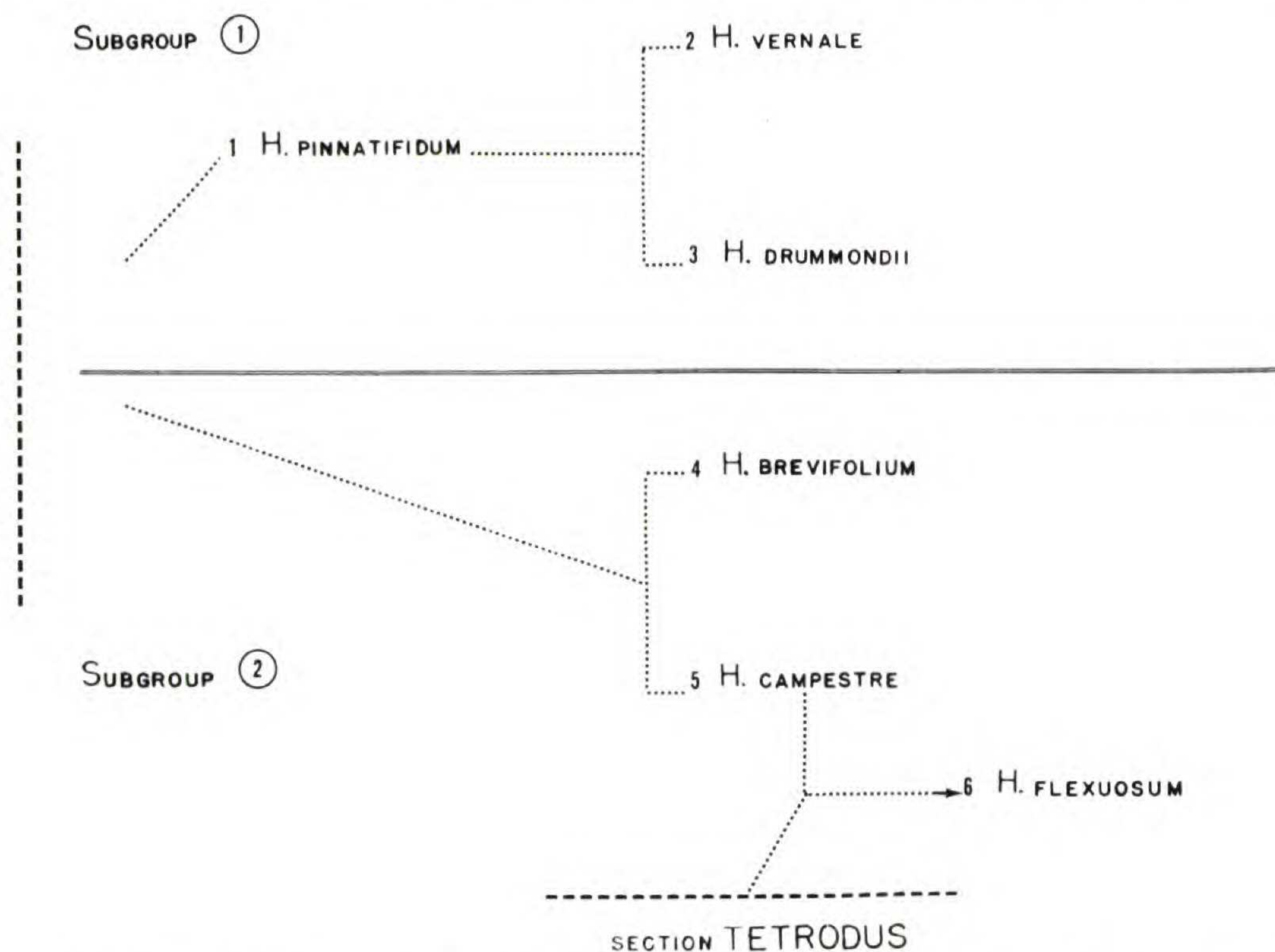
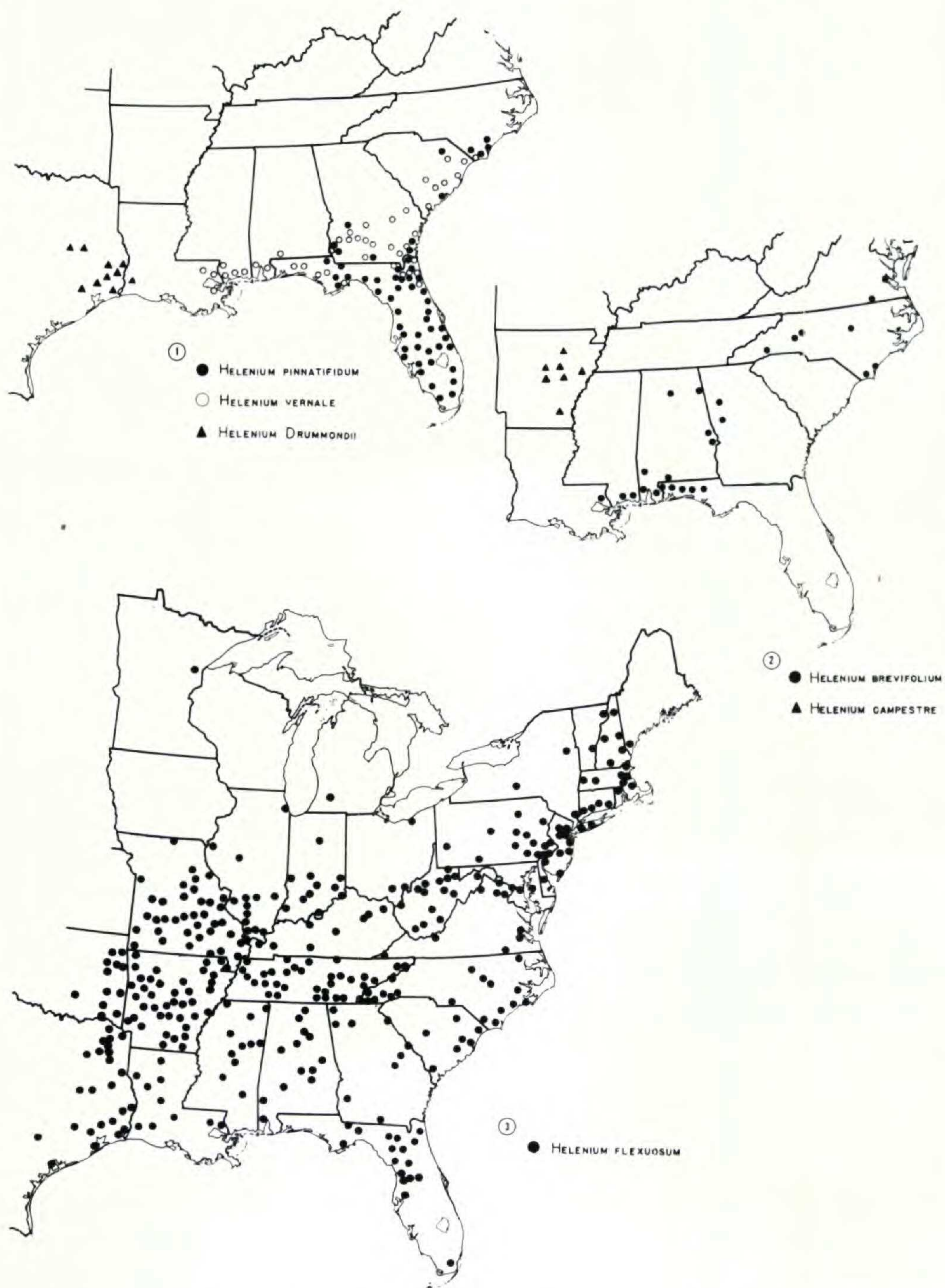


FIGURE 7. Diagrammatic scheme of the supposed phyletic sequence within the Section LEPTOPODA.

DISTRIBUTION OF THE TAXA AND GEOLOGICAL CONSIDERATIONS

While a phylogenetic scheme based on morphological characters has an inherent significance, it becomes more significant when it is integrated with the distribution of the taxa involved and some of the geological history of the area that these taxa occupy. Map 1 presents the distribution of the three taxa placed in subgroup 1. It demonstrates that all three of these taxa are restricted to the Coastal Plain Province of southeastern United States. Maps 2 and 3 give the distribution of the taxa of the second subgroup and they reveal a distribution that is



MAPS 1-3. Distribution of the taxa in Section LEPTOPODA. Map 1. *Helenium pinnatifidum*; *Helenium vernale*; *Helenium Drummondii*. Map 2. *Helenium brevifolium*; *Helenium campestre*. Map 3. *Helenium flexuosum*.

either Piedmont-Coastal Plain or Piedmont, with the exception of the widespread *Helenium flexuosum*.

The distribution of *H. pinnatifidum* (Map 1) shows a break in the Georgia-South Carolina border area, so that the total species distribution can be considered as being composed of two segments; one of which is essentially of Florida and Georgia and the other of North and South Carolina. This break in the distribution of a taxon or taxa at approximately the Savannah River has been noted in other genera of the *Compositae* (*Marshallia*, *Balduina*) and in *Sabatia* and *Rhynchospora*. Despite this effective division of *H. pinnatifidum* into two distributional segments, no differences between these two segments could be established which were either consistent or definitive. The slight differences in aspect that did seem to exist, namely a less robust habit, are attributed to climatic effects on the Carolina segment in contrast to the climatic conditions that prevail upon the Florida segment. Such differences do not seem to warrant taxonomic distinctions. Perhaps transplant studies and other biosystematic techniques may reveal a basis for recognition of infraspecific taxa in *H. pinnatifidum*. However, until this is demonstrated, *H. pinnatifidum* is treated here as a species without formal or clearly recognizable infraspecific taxa.

Helenium vernale (Map 1) is partly sympatric with *H. pinnatifidum*. However, no evidence of hybridity between these two species was noted in the specimens examined or from field studies. Moreover, *H. vernale* has a flowering peak that occurs approximately two weeks later than that of *H. pinnatifidum*, where the two are sympatric. The distribution of *H. vernale* is for the most part complementary to that of *H. pinnatifidum* as might be expected of two closely allied though distinct taxa. The remarks to be made concerning *H. Drummondii* are reserved and will be made along with those concerning *H. campestre*. At this point, however, it is to be noted that while the distribution of *H. Drummondii* (Map 1) is restricted to essentially eastern Texas and is independent of the distribution of *H. pinnatifidum* and *H. vernale*, it does conform to the pattern of distribution for all three of these taxa in being restricted to the Coastal Plain.

The distribution of *Helenium brevifolium*, although it appears to be extensive on the basis of the plotted locations in Map 2,

is considered to be a restricted type. The inland locations and those of the Atlantic Coastal Plain are a particular kind of habitat. In all the cases where *H. brevifolium* occurs away from the Gulf Coastal Plain, it inhabits either bogs in the Atlantic Coastal Plain or else coastal-plain-like bogs of the Piedmont. This restricted kind of habitat and distribution is considered to be a relic type of distribution, in which an originally Coastal Plain species has persisted in the Piedmont only in those habitats that are similar to the conditions of the Coastal Plain. The occurrence of this Coastal Plain-Appalachian type of distribution has generally been accepted as being correlated with the Schooley peneplane of the Miocene. With the uplift of this peneplane and the change from a coastal-plain-like aspect, plant migrations apparently kept pace with the migration or restriction of the Coastal Plain. However, relic populations seem to have been left behind on the uplifted portion where the environment was suitable for their survival. The distribution of *H. brevifolium* on the Carolina Coastal Plain and the Gulf Coastal Plain would seem to indicate that it had been able to keep pace with the migration or restriction of the Coastal Plain in at least two areas. The presence of *H. brevifolium* in greatest abundance in the Gulf Coastal Plain is taken to indicate its primary affinity with the Coastal Plain. This is corroborated further by the fact that *H. brevifolium* occupies several kinds of habitats in the Gulf Coastal Plain—savannahs, pine barrens, bogs, flat woods, ditches and pocosins—in contrast to the restricted boggy habitats occupied in the Piedmont. The lack of any known relic populations of either *H. vernale* or *H. pinnatifidum* in the Appalachian Piedmont is interpreted to mean that they have been unable to survive there, if left as relics, and that these species, *H. pinnatifidum* and *H. vernale*, are more obligate Coastal Plain species.

The restricted distribution of *H. brevifolium* on the Atlantic Coastal Plain, occurring only in North Carolina and Virginia, appears to be due to a secondarily imposed restriction. In the case of the Virginia populations of *H. brevifolium*, the climatic conditions of that area probably limit its distribution. Although it is the Coastal Plain, the climate and environment are roughly equivalent to those of the inner Carolina Piedmont. The southeastern North Carolina populations appear to be limited for another reason. *H. brevifolium* here occupies a climatic

area that is more favorable than that of the Carolina Piedmont. However, in the southeastern North Carolina locations, *H. brevifolium* is in competition with *H. vernale* and *H. pinnatifidum*. It seems that *H. brevifolium* is not able to compete with these other two for the favorable habitats and thus is unable to spread southward along the Coastal Plain or even to move out of the bogs that it does occupy. Actually, all three species, *H. vernale*, *H. pinnatifidum* and *H. brevifolium*, appear to be surviving under near-marginal conditions in the North Carolina-Virginia area.

It can be noted from the maps that the areas which support the greatest number of species of the Section LEPTOPODA are the Appalachicola-Chattahoochee River section of Alabama, Florida and Georgia and, secondly, the southeasternmost counties of North Carolina. Geological maps devoted to the advance and retreat of the seas during Pleistocene glaciation and interglacial stages indicate that the Appalachicola-Chattahoochee River area most probably was not inundated completely during the Pleistocene. If so, this area may well have served as a "refuge" for these species that have a Coastal Plain distribution east of the Mississippi River and the more widespread occurrence of these species today may be due to post-Pleistocene migrations away from this area. The idea of considering the North Carolina location as a second "refuge" is tempting. However, though the author has heard that the North Carolina Cape Fear region or a place somewhat to the east of it was not inundated during the Pleistocene, he has been unable to uncover any published account to that effect.

The restricted distribution of *H. Drummondii* (Map 1) to the Coastal Plain of eastern Texas and the restricted distribution of *H. campestre* (Map 2) to the Piedmont of the Ozarks and Ouachita Mountains in Arkansas, both west of the Mississippi and apart from the main distribution of the Section LEPTOPODA, appear to be more than coincidence. The partition in the distribution of these five species shows a positive correlation with the geological phenomenon known as the Mississippi Embayment of the Eocene. If this correlation reflects an actual event in the history of these species, then the Mississippi Embayment has probably served as an isolating agency that has indirectly led to the formation of *H. Drummondii* and *H. campestre*. Presumably, the prototypes of these two species

were segregated from the main distribution of *H. pinnatifidum*-*H. vernale* and *H. brevifolium*. Since then, development within these geographical segregates has proceeded along sufficiently independent lines leading to the formation of two new species. The morphological distinctness of these two species, *H. Drummondii* and *H. campestre*, along with their obvious relationship to *H. pinnatifidum*-*H. vernale* (for *H. Drummondii*) and *H. brevifolium* (for *H. campestre*) would seem to indicate that *H. Drummondii*-*H. vernale* and *H. campestre*-*H. brevifolium* are vicarious species-pairs.

These vicarious species-pairs provide a reasonable basis for some speculations concerning the history of the Section LEPTOPODA. The fact that a vicarious species-pair occurs in both subgroups suggests that these subgroups have been long-established and probably were functional units prior to the Mississippi Embayment. Moreover, the fact that the morphological characters that serve to define the Section LEPTOPODA are equally expressed in all five members of this section (excluding *H. flexuosum* from consideration) indicates itself that the "Leptopoda" tendency had probably been in existence prior to the Eocene and that the section is an exceedingly natural group.

If these geological-geographical correlations are to be taken at face value, then it seems certain that the *Compositae* were in existence by the Eocene and probably earlier than that. Such a statement is not supported by the fossil record, however, but this is hardly a cause for concern. The herbaceous nature of the *Compositae* for the most part would exclude their being a very good or likely source of fossil material. Another means of time-dating, the pollen record, has also failed to indicate the existence of the *Compositae* in the Eocene. The fact that the *Compositae* are predominantly adapted to insect pollination makes the presence of *Compositae* pollen along with wind-borne pollens in peat deposits highly unlikely.

If *Helenium flexuosum* (Map 3) came into being as a result of hybridization between *H. campestre* and some member of the annual-biennial species of *Helenium* from Texas-Mexico, as it is believed, then its origin must necessarily be later than that of either of the parental species. *Helenium campestre*, it has been pointed out, would seem to have been evolved at sometime since the Eocene, being indirectly formed through

the agency of the Mississippi Embayment. In relation to the annual-biennial taxa, the increasingly arid conditions postdating the Miocene have been suggested by many authors as the period in which the annual-biennial habit was evolved in many perennial taxa. Assuming that this is so and with an area of northern Mexico-southwestern Texas as a center of origin for the annual-biennial taxa of *Helenium*, post-Miocene time would have witnessed an increasing degree of distribution and speciation of the annual-biennial taxa of *Helenium*.

Presently, the ranges of distribution of *Helenium campestre* and the annual-biennial taxa are not sympatric. The closest known location of any of the annual-biennial taxa to that of *H. campestre* is the occurrence of the plant known as *Helenium elegans* DC. in Hempstead County of southwestern Arkansas. This location is one hundred miles or more away from the nearest known location of *H. campestre*. Within a distance of two hundred miles, however, *H. elegans* is firmly established in the northeastern part of Texas. These presently known distributions of the two taxa, *H. campestre* and *H. elegans*, are not close enough to reasonably assume that hybridization has taken place under the prevailing conditions.

Despite the present conditions, it is entirely possible that the distribution of these two plants may have been sympatric during some past time. Such a time might well have been during the Pleistocene. During the Pleistocene, extensive plant migrations have generally been conceded to have occurred. It would seem probable that such shifts in distribution attendant on the climatic conditions of the Pleistocene, during both the glacial and interglacial stages, may have brought the two components, *H. elegans* and *H. campestre*, into contact. It is presumed that it was at such a time that hybridization between these two occurred, and that *Helenium flexuosum* came into being as the hybrid product. It would also seem that it was during this time that *H. campestre* became introgressed with some of the genetic material of *H. elegans*. Subsequent to this period of contact, the two parental taxa have become allopatric, seemingly through the increasingly more restricted distribution of *H. campestre*.

The hybrid product *Helenium flexuosum*, however, apparently had conferred upon it a wide range of tolerances and has since

become something of a weed. The distribution of *Helenium flexuosum*, as Map 3 exhibits, is the most extensive of any species in the section LEPTOPODA and within this range a wide variety of ecological conditions is encountered. Perhaps significantly enough, the most dense degree of distribution of *Helenium flexuosum* appears to be in the Arkansas-Missouri-Tennessee region.

Finally, to stretch a correlation, it can be noted that the distribution pattern of the perennial, neutral-rayed Section LEPTOPODA and the perennial, styliiferous-rayed species of *Helenium* is correlated with the submergence of the Late Cretaceous Period. At this time, with the submergence of Texas and eastern Mexico and the progressive development of the Mesocordilleran Sea, the land mass of North America is supposed to have been divided into two areas: a central-eastern area and the Mesocordilleran region of western America. Provided the *Compositae* were in existence at that time and that the genus *Helenium* had been expressed to some degree, such a geological occurrence might well have been the precipitant factor leading to the formation of the perennial, neutral-rayed species in the east and the perennial, styliiferous-rayed species of the West Coast, Arizona, and western and central Mexico. In accordance with this, and on the basis of morphological features as well, the extremely widespread (northern-transcontinental) perennial species *H. autumnale* and the annual-biennials of Texas and Mexico probably had a much later origin from these perennial species of the western land mass.

These speculations concerning the evolution of the Section LEPTOPODA and their correlation with the geological sequence of events may be summarized in the following manner:

1. End of the Cretaceous Period.—The Section LEPTOPODA and the styliiferous-rayed portion of *Helenium* (or their precursors) appear to have existed as separate tendencies.

2. Eocene Epoch.—The Mississippi Embayment apparently served as an isolating agency between populations of certain species in both morphological subgroups of the Section LEPTOPODA. These segregated portions then pursued a more or less independent course of evolution resulting in the formation of a vicarious species-pair in both of the subgroups.

3. Miocene Epoch.—Uplift of the Schooley Peneplane and

the subsequent climatic changes induced a more restricted distribution of the species of LEPTOPODA, with the formation of relic populations in the Appalachian highlands (i. e. *Helenium brevifolium*) on one hand and a distribution restricted to Coastal Plain areas on the other hand. Likewise, post-Oligocene aridity possibly induced the formation of the annual-biennial habit within the genus *Helenium*, resulting in the evolution and distribution of the Section TETRODUS, centered on Texas-Mexico.

4. Pleistocene.—The climatic fluctuations during the glacial and interglacial stages of the Pleistocene apparently influenced the distribution of both the annual-biennial taxa and *Helenium campestre* to the extent that their distributions became sympatric to some degree. During this time of contact, *Helenium flexuosum* came into being as a hybrid product between the two. During the Pleistocene, the fluctuating sea level must have had its effect on the distribution of those species that inhabited the Coastal Plain. Either successful migrations were made by these species, keeping pace with the restriction and shifting of the Coastal Plain or else certain areas served as “refugia” for these species. From these refugia, never quite inundated by the rising interglacial seas, the species of LEPTOPODA re-occupied the Coastal Plain since the Pleistocene. The Apalachicola-Chattahoochee River section of Alabama, Florida and Georgia seems to be indicated as one of these refugia. A second possible refugium may have been located in the southeastern part of North Carolina, the Cape Fear region, or some area just east of there but now eroded and reduced below sea level.

SPECIES CONCEPTS

The six species of the Section LEPTOPODA have posed very few problems along lines related to species concepts. Each of the species is marked by absolute discontinuities of morphology from any of the other five. Indeed, these discontinuities between the species do not rest on a single character but on several characters so that none of the species should be confused with another. Where the author has merged previously recognized taxa, without taxonomic recognition of the former segregate, he has presented evidence for such a course. This is presented with each species discussion in the systematic section of this paper.

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ARIZ, University of Arizona; BKL, Brooklyn Botanic Garden; CHARL, Elliott Herbarium of the Charlestown Museum; CLEMS, Clemson Agricultural College; COLO, University of Colorado; CS, Colorado Agricultural and Mechanical College; DS, Stanford University; DUKE, Duke University; DWC, Darlington Herbarium, Pennsylvania State Teachers College; EW*, Herbarium of Joseph Ewan, Tulane University; F, Chicago Natural History Museum; FLAS, Florida Agricultural Experiment Station, University of Florida; G, Conservatoire et Jardin Botaniques, Geneva; GA, University of Georgia; GH, Gray Herbarium, Harvard University; IA, State University of Iowa; IDS, Idaho State College; LS, Herbario de la Salle, Colegio de la Salle, Habana; LUNDELL, Texas Research Foundation; MEXU, Universidad Nacional de Mexico, Mexico City; MICH, University of Michigan; MIN, University of Minnesota; MO, Missouri Botanical Garden; MONTU, Montana State University; MV*, Herbarium of Marie-Victorin, University of Montreal; NCSC, North Carolina State College;

² The Herbaria of the World. Pt. 1. Regnum Vegetabile, Utrecht, Kemink en Zoon, 2: 1954.

NCU, University of North Carolina; ND, University of Notre Dame; NDA, North Dakota Agricultural College; NEBC, New England Botanical Club Herbarium; NMC, New Mexico Agricultural and Mechanical College; NMEX*, University of New Mexico; NO, Tulane University; NY, New York Botanical Garden; OKL, University of Oklahoma; OKLA, Oklahoma Agricultural and Mechanical College; OSC, Oregon State College; PENN, University of Pennsylvania; PH, Philadelphia Academy of Natural Sciences; POM, Pomona College; RENO, University of Nevada; RM, University of Wyoming; RSA, Rancho Santa Ana Botanic Garden; SDC, South Dakota State College; SMU, Southern Methodist University; SV, Estacion Experimental Agronomica, Habana; TAES, Agricultural and Mechanical College of Texas; TENN, University of Tennessee; TEX, University of Texas; UARK, University of Arkansas; UC, University of California; US, United States National Museum; USC*, University of South Carolina; WIS, University of Wisconsin; WS, State College of Washington; WVA, West Virginia University.

SYSTEMATIC TREATMENT

Helenium Section **Leptopoda** (Nutt.) A. Wood

Leptopoda Nutt. Gen. N. A. Pl. **2**: 174. 1818.

Leptophora Raf. Am. Mo. Mag. Crit. Rev. **4**: 195. 1819;
Jour. Phys. Chim. Hist. Nat. **89**: 260. 1819.

Leptocarpha Raf. ex Endl. Gen. p. 1383. 1841.

Helenium Sect. LEPTOPODA (Nutt.) A. Wood. Am. Bot. & Fl. **180**. 1870.

Helenium Sect. *Leptopoda* (Nutt.) Gray. Proc. Am. Acad. **9**: 204. 1874.

Perennial, vernal herbs of the southeastern United States; foliage and stems glabrous or pubescent; monocephalous or polycephalous; simple, corymbosely or paniculately branched. Radical leaves sessile or petioloid; cauline leaves decurrent. Peduncles glabrous, pubescent, lanose or tomentose. Ray florets neutral and sterile, yellow (-bicolor, red-brown); disk florets hermaphroditic, yellow or red-brown (-sordid). Pappus scales elliptic-lanceolate, oblanceolate, obovate, suborbicular; obtuse and unawned or acute and/or awned; entire, erose or fimbriate; sessile or clawed. Achenes glabrous, hairy-pubescent or puberulent. TYPE SPECIES of the section: *Leptopoda Helenium* Nutt.

A. Heads radiate; the rays well developed, yellow or occasionally red-brown or bicolored (red-yellow).

B. Disk yellow; plant unbranched; usually monocephalous; plants of the Coastal Plain.

C. Pappus scales elliptic-lanceolate to elliptic-oblanceolate, the margin entire, erose or at most merely lacerate.

D. Peduncles decidedly pubescent; achenes pubescent; mid-cauline leaves hardly decurrent, the wing not exceeding 5 mm. in length; radical leaves not petioloid but usually pinnatifid. .1. *Helenium pinnatifidum*.

- D. Peduncles glabrous, rarely glabrate; achenes glabrous; mid-cauline leaves manifestly decurrent, the wings much exceeding 5 mm. and usually extending from node to node; radical leaves petioid, rarely pinnatifid-incised, usually repand to denticulate. 2. *Helenium vernale*.
- C. Pappus scales oblong to oblong-cuneate, deeply slashed into many capillary segments, the segments (*fimbriae*) comprising $\frac{1}{2}$ or more of the total pappus scale body and crimped at maturity. . . . 3. *Helenium Drummondii*.
- B. Disk red-brown; plant branched; heads few to many; plants of the Piedmont, Piedmont-Coastal Plain or widespread over the eastern portion of the United States.
- E. Pappus scales obovate to suborbicular, unawned and non-costate; plant corymbosely branched; disk corollas pentamerous.
- F. Basal leaves glabrous; stem glabrous below; pappus scales obovate, more or less clawed, 1.0 mm. or more in length; achenes hairy-pubescent. 4. *Helenium brevifolium*.
- F. Basal leaves hairy-pubescent; stem hairy-pubescent below; pappus scales obovate to suborbicular, not clawed, 0.5 mm. or less in length; achenes puberulent. 5. *Helenium campestre*.
- E. Pappus scales lanceolate to elliptic-lanceolate, more or less awned and costate; plant paniculately branched; disk corollas predominantly quadrimerous, with 4 lobes and 4 stamens. 6. *Helenium flexuosum*.
- A. Heads discoid, disk color red-brown. 6. *Helenium flexuosum*.

1. *Helenium pinnatifidum* (Nutt.) Rydb.

Galardia fimbriata Michx. Fl. Bor.-Am. **2**: 142. 1803. Syntype: Collected by Michaux prior to 1796 in Carolina and Georgia (P), not examined in entirety; photograph of syntype (GH) seen. *Synonym pro parte*.

Leptopoda puberula MacB. in Ell. Sk. Bot. S. C. & Ga. **2**: 445. 1823. Lectotype: Collected by MacBride, Florida (CHARL).

Leptopoda fimbriata (Michx.) A. Eaton, Man. Bot. N. A. 275. 1829 non T. & G. Fl. N. A. **2**: 387. (1842).

Leptopoda pinnatifida Nutt. Trans. Am. Phil. Soc. ser. 2. **7**: 372. 1841. Lectotype: Collected by Baldwin in East Florida (PH).

Leptopoda incisa T. & G. Fl. N. A. **2**: 387. 1842. Holotype: Collected by LeConte in Georgia (NY); isotype ? (PH).

Leptopoda puberula MacB. in Ell. var. *pinnatifida* (Schw.) T. & G. Fl. N. A. **2**: 387. 1842.

Helenium incisum (T. & G.) A. Wood, Am. Bot. & Flor. 182. 1870.

Helenium fimbriatum A. Wood, Am. Bot. & Flor. 182. 1870. ? *nomen ambiguum*.

Helenium puberulum (MacB. in Ell.) A. Wood, Am. Bot. & Flor. 182. (1870) non DC. Prodr. **5**: 667. 1836.

Helenium Nuttallii A. Gray var. *incisum* (T. & G.) A. Gray, Proc. Am. Acad. Arts & Sci. **9**: 204. 1874.

Helenium vernale Nutt. ex A. Gray, Proc. Am. Acad. Arts & Sci. **9**: 204 (1874) non Walt. Fl. Carol 210. 1788.

Heleniastrum fimbriatum (Michx. [A. Gray]) O. Ktze. Rev. Gen. (pt. 1) 342. 1891.

Helenium incisum (T. & G.) Small, Fl. SE. U. S. 1292. 1903. Superfluous name.

Helenium pinnatifidum (Schw.) Rydb. N. A. Fl. **34** (2): 130. 1915.

Helenium vernale auct. non Walt. Fl. Carol. 210. 1788.

Perennial herb, the stem developing from a rosette formed the previous season from the seedling or as an offset from the short caudex; caudex with coarse fibrous roots and often with the persistent fibrous leaf remnants of the prior rosettes. Plant erect, (3-) 4.5-6.0 (-8) dm. in height, single-stemmed, often occurring in clusters, *unbranched and usually monocephalous*, occasionally with two heads and very rarely with three. When the number of heads is greater than one, the secondary heads, arising from buds within the upper leaf axils, are formed at a later period than the terminal one and are decidedly later in flowering than the primary head, as well as being borne on shorter peduncles. Stems sulcate and often anthocyanaceous below, becoming increasingly striate and pubescent above. *Peduncle* striate, decidedly *pubescent at the base of the involucre*, becoming enlarged and fistulous beneath the involucre. Leaves glabrous, strongly uninerved to obscurely 3-nerved, impressed-punctate and resin-atomiferous, becoming reduced in size and form upwards, so the plant appears scapose, especially when viewed in the field. Radical leaves usually intact and present, (3-) 4.5-8.0 (-19) cm. in length, 0.3-1.1 cm. in width; being linear- or elliptic-lanceolate to spatulate, oblanceolate or obovate in outline; margin ranging from merely repand through coarsely and remotely dentate, crenate to pinnatifid; apex obtuse to acute and the bases enlarging somewhat within the rosette so as to become partially clasping, *but with the lower portions of the leaves not contracted so as to be petioloid in form*. Lower cauline leaves (1.2-) 3.5-6.0 (-7) cm. in length, (0.1-) 0.4-0.6 (0.8) cm. in width; linear to linear-lanceolate in outline; margin and apex much the same as in the radical leaves, sessile and with the leaf bases broadly inserted and *not decurrent* along the stem. Mid-cauline leaves becoming more reduced with each successive internode, and essentially the same as the lower cauline with the exception that *the mid-cauline leaves are the only ones of the plant that are decurrent and then only weakly so*, the leaf bases somewhat flared at the insertion so as to be semi-amplexicauline, *the bases being shortly decurrent 0.1-0.5 cm. in length*. Upper cauline leaves reduced to bracteate appendages; linear or linear lanceolate in outline and more or less toothed on the margin; not decurrent, and becoming more remote in disposition with increased position upwards. Involucre biseriate, the outer series exceeding the inner series; phyllaries lanceolate, (4.0-) 5.0-6.0 (-8.0) mm. long, 1.0-1.5 mm. wide at the base, apex acute, pubescent, patent initially, withering with age.

and either reflexed or not. Heads convex to depressed-hemispherical, 0.5–1.2 cm. in height, 1.0–2.5 cm. in width; receptacle convex to hemispherical. Ray florets neutral; ligules yellow, 5.0–15.0 mm. long, cuneate, 3(–4)-fid at the apex, pubescent below, resin-atomiferous; achenes abortive and less than the length of the disk achenes. *Disk yellow*; disk florets fertile; corollas 5-lobed, 3.0–5.0 mm. in length, glandular-pubescent on the lobes, resin-atomiferous, cylindric to cylindric-campanulate in outline with a short basal tube; pappus scales oblong to elliptic-oblong, 1.0–2.0 mm. in length, 5–10 in number, *margin erose to lacerate with age*, apex obtuse, though often apiculate to aristillate; achenes 1.5–2.0 mm. long, *hairy on the ribs*, resin-atomiferous, columnar to truncate-turbinate.

DISTRIBUTION: Plants of the Atlantic and Gulf Coastal Plain of the southeastern United States; occurring in wet pine barrens, moist flatwoods, moist savannahs, pine-barren pond margins, roadside ditches and their banks, railroad ditches, borrow pits, pine and marl prairies, cypress ponds and swamps, the everglades; throughout most of Florida except for the westernmost part of the panhandle, northward into Georgia in the Chattahoochee drainage area and along the Atlantic coastal areas into the southeastern counties of North Carolina. (MAP 1)

REPRESENTATIVE SPECIMENS.—Florida. Alachua Co.: Fairbands, *Correll & Correll 8945* (DUKE). Baker Co.: Sapp, 25 April 1940, *West & Arnold s.n.* (FLAS). Bradford Co.: Lawtey, 25 March 1940, *Murrill s.n.* (MO). Brevard Co.: Indian River, *Palmer 294* (F, GH, MO). Broward Co.: W. of Pompano, *Moldenke 392a* (DUKE, MO, NY, PENN). Charlotte Co.: pine slough, 21 April 1947, *Frye s.n.* (FLAS). Citrus Co.: 3 m. S. of Red Level, 15 March 1945, *West, Arnold & St. John s.n.* (FLAS). Clay Co.: Hibernia, March 1869, *Canby s.n.* (DS, F, GH, MO, NY, US). Collier Co.: Big Cypress, 16 m. E. of Immokalee, 4 March 1919, *Sheehan s.n.* (NY). Dade Co.: 10 m. SW. of Miami, *O'Neill 7597* (ARIZ, DS, EW, F, ND, NY, POM, RM, US). Duval Co.: near Jacksonville, *Curtiss 1518* (F, FLAS, GH, IA, MIN, MO, NY, OSC, PH, SMU, UC, US). Dixie Co.: 9 m. W. of Cross City, 29 March 1936, *Humm & West s.n.* (FLAS). Flagler Co.: N. of Andulasia, 18 April 1940, *West & Arnold s.n.* (FLAS). Franklin Co.: Apalachicola, *Chapman 2508a* (GH, MIN, MO, NCU, NY, PENN, US). Gadsen Co.: 10 m. W. of Chattahoochee on Rte. 90, *Sargent 6079* (OKLA, RM, SMU). Glades Co.: Lakeport, *Lovett 258* (DUKE). Hardee Co.: Cattle Range Station near Limestone, 17 April 1942, *Kirk s.n.* (FLAS). Highlands Co.: Sebring, *Hunnewell 9059* (GH). Hillsborough Co.: Tampa, *Britton, Britton & Shafer 25* (NY). Indian River Co.: Felsmere, *Small 8865* (NY). Jackson Co.: 5 m. E. of Marianna, *Hood 1549* (FLAS). Lafayette Co.: cypress pond S. of Mayo, 21 May 1941, *West & Arnold s.n.* (FLAS). Lee Co.: vicinity of Fort Myers, *Standley 3* (F, GH, MO, NY, US). Levy Co.: vicinity of Sumner, *Miller 376* (US). Liberty Co.: Bristol, March 1890, *Canby s.n.* (MIN, PH). Manatee Co.: Bradentown, *Tracy 7420* (GH, NY, US). Monroe Co.: S. of Pinecrest, 9 Jan. 1942, *Davis s.n.* (FLAS). Nassau Co.: Callahan, 5 April 1945, *Knight s.n.* (FLAS). Okeechobee Co.: Bassenger, *Howell 1047* (US). Orange Co.: 3 m. NE. of Winter Park, *Walker 1758* (PH). Osceola Co.: Kissimmee, *Bitting 325* (F, FLAS, MO). Palm Beach Co.: Earman, *Randolph 16* (GH). Pasco Co.: near Ehren, *Barnhart 2711* (F, NY). Polk Co.: 5 m. S. of Lakeland, *Blanton 6973* (DS, MICH, MO, ND, PENN, POM, RM, US). Putnam Co.: low pine barrens, Palatka, March 1882, *Mohr s.n.* (UARK). St. Johns Co.: St. Augustine,

April 1875, *Reynolds s.n.* (BKL, F, MICH, NY, PENN, PH, WIS). St. Lucie Co.: Fort Pierce, *Hunnewell 7482* (GH). Sarasota Co.: Osprey, 12 March 1904, *Smith s.n.* (DUKE). Seminole Co.: Lake Munroe, March 1876, *Garber s.n.* (PH, US). Taylor Co.: 4 m. NE. of Penholloway, *Hubricht B2079* (MO). Union Co.: 2 m. S. of Raiford, 22 May 1942, *West & Arnold s.n.* (FLAS). Volusia Co.: Lake Helen, 12 April 1910, *Hood s.n.* (FLAS, MO). Wakulla Co.: Medart, *Moldenke 1125* (DUKE, MO, NY, PENN). **Georgia.** Camden Co.: 1 m. NE. of Colrain, *F. Harper 1408* (PH). Early Co.: between Cedar Springs and Saffold, *R. M. Harper 3638* (GH, MO, NY^a, US^a; *not* 1, NY^b, MICH, PH, US^b). Glynn Co.: 2 m. N. of Little Satilla River, Rte. 17, *Correll & Correll 8770* (NCSC, US). Lowndes Co.: along the A. C. L. Railroad, 3 m. E. of Valdosta, *Quarterman 498* (DUKE). Miller Co.: 2 m. W. of Colquitt, *Thorne 3414* (IA). Sumpter Co.: 1 m. S. of Cobb, *R. M. Harper 2213* (F, GH, MO, NY, US). **South Carolina.** Charleston Co.: Owensdew, S.W. E-2, 22 April 1944, *Hunt, Duncan & Martin s.n.* (GH). Darlington Co.: Black Creek W. of Hartsville, 24 April 1921, *Norton s.n.* (NCU). **North Carolina.** Brunswick Co.: between Southport and Supply, *Godfrey 52273* (DUKE, FLAS, MO, NCSC, SMU). Columbus Co.: near Bolton, *Weatherby 6104* (DUKE, GH, NY, PENN, US). New Hanover Co.: near Carolina Beach, *Godfrey & White 7105* (DUKE, GH, MIN, MO, NY, PH, UC, US). Pender Co.: about ½ m. N. of Burgaw, *Radford & Stewart 203* (NCSC, NCU, TEX, UC). The locations of the following specimens from North Carolina are believed to be erroneous: Rowan Co.: Salisbury, May 1882, *M. E. Hyams* (NY); Iredell Co.: ex herbario Eli Lilly & Co., *Hyams* (MO, NY).—M. E. Hyams is known to have been an herb collector and his home was apparently at Statesville, Iredell Co., North Carolina. Statesville was also the location of an herbarium devoted to drug plants. These extreme inland locations are certainly doubtful on the basis of the remaining distribution of this species. In all probability, the origin of these specimens was from the Coastal Plain of North Carolina, a location known to have been visited by Hyams. The author made a search of several Coastal Plain-like bogs in Iredell Co., N. C. in an effort to locate this species there but such efforts were unfruitful, although populations of *Helenium brevifolium* were located in some of these bogs.

The name *Helenium vernale* has been consistently misapplied to this taxon. The results of this continuous misapplication have been twofold: the displacement of the proper name and the continued propagation of the synonym *H. Nuttallii* A. Gray as the proper name for *H. vernale* Walt. (cf. RHODORA 58: 311–317. 1956.) Consequently, this species must have its rightful name restored to it and *H. vernale* Walt. must be associated with its nomenclatural type and regain its correct position as the legitimate name for the taxon known of late as *H. Nuttallii*.

The earliest name that is both legitimate and validly published for the present species is *Galardia fimbriata* Michx. After a study of photographs of the specimens on which this name is based—supplemented by data provided by Monsieur Leandri of the Muséum National d'Histoire Naturelle concerning the

actual specimens—and in conjunction with an analysis of the original description, it has been determined that the specimens on which the name *Galardia fimbriata* is based belong to two different taxa. Michaux's description is so generalized as to encompass both elements. One of these elements is *Helenium vernale* Walt. dating from 1788. The remaining element is to be associated with the name *Galardia fimbriata* Michx. dating from 1803.

In 1829, Amos Eaton transferred *Galardia fimbriata* Michx. to *Leptopoda* (Man. Bot. N. A. 275. 1829.) Although Eaton misattributed the authority of *Galardia fimbriata* to Willdenow, the footnote referring to the new combination “[*Leptopoda*] *puberula*, Macbride. *Galardia*, Mx.” clearly indicates the basionym and the combination is to be written as *Leptopoda fimbriata* (Michx.) A. Eaton. In 1842, Torrey and Gray (Fl. N. A. 2: 397.) published the later homonym *Leptopoda fimbriata* T. & G. Following the description of this species they cite: “—*Galardia fimbriata* Michx. fl. 2. p. 142?” As the distribution of this species they list: East Florida, based on a specimen collected by Leavenworth; and Texas, based on specimens collected by Drummond and another specimen collected by Leavenworth. The distribution of *Galardia fimbriata* given by Michaux is: “in paludosis apricis, a Carolina ad Floridam.” In the comments which accompany the description, Torrey and Gray state: “This is very probably not the *Galardia fimbriata* of Michaux, although it best accords with his character; but since that name cannot properly be employed for either of the two species already described, it may in any case be adopted for the present very distinct species, for which it is very appropriate.” The fact that Torrey and Gray cite Michaux with a query and the two phrases “is very probably not” and “may in any case be adopted” indicate that Torrey and Gray were not transferring *Galardia fimbriata* into *Leptopoda* but rather were establishing a new species with the epithet *fimbriata*, based on the Leavenworth and Drummond material. As a later homonym of *Leptopoda fimbriata* (Michx.) A. Eaton, the *Leptopoda fimbriata* of Torrey and Gray is, of course, illegitimate.

In 1870, Alphonso Wood merged the genus *Leptopoda* with *Helenium* and made the combination *Helenium fimbriatum*.

There is no direct indication made by Wood as to which of the three possible combinations of the epithet *fimbriata* served as the basionym in this new combination; i.e. *Galardia fimbriata* Michx., *Leptopoda fimbriata* (Michx.) A. Eaton, or *Leptopoda fimbriata* T. & G. This name, *Helenium fimbriatum* A. Wood, however, under the provisions of Article 65 of the Code, has been declared to be an ambiguous name and is rejected from use in the genus *Helenium*. The discussion related to this action is to be found within the treatment given to *Helenium Drummondii* in this paper.

The next available name is *Leptopoda puberula* MacB. in Ell. However, in transferring this epithet to *Helenium*, Wood created a later homonym to that of DeCandolle and this name must be rejected under the injunction of Article 64. Chronologically, *Leptopoda pinnatifida* Nutt. has priority over the remaining names that apply and the epithet *pinnatifidum* is the legitimate one for this species. However, the circumstances surrounding the publication of *Leptopoda pinnatifida* require clarification.

Nuttall, using his customary format in publishing names that he considered new to science, did so in the following fashion: "*Leptopoda* * *pinnatifida*; . . ." with the asterisk indicating a new name and the semicolon indicating that the description is to follow. Just after the semicolon, in the case of *L. pinnatifida* however, Nuttall included in parenthesis, "; (Herb. Schw.)." Even though the type specimen bears no reference to DeSchweinitz, it would appear that Nuttall intended this reference to DeSchweinitz to indicate only that the specimen for this new name came from DeSchweinitz's herbarium. Moreover, the type does not bear the inscription "pinnatifida" in any hand other than Nuttall's own so that the epithet cannot be considered to be a manuscript name picked up by Nuttall. Indeed, the type specimen has a label which repeats Nuttall's characteristic format and there is no indication that the herbarium specimen was ever in DeSchweinitz's hands. Moreover, there is no specimen of *Leptopoda pinnatifida* amongst the Nuttall material at the British Museum which might refute such an interpretation or indicate prior ownership by DeSchweinitz. Actually, a specimen that does bear a reference to DeSchweinitz is a syntype of *Helenium brevifolium* Nutt. at the

Philadelphia Academy of Natural Sciences which has the notation "in Herb. Schw. sub nomine *Rudbeckia* (Yadkin)."

In the *Flora of North America* (1842) and in the *Synoptical Flora* (1884) the epithet *pinnatifida* is attributed to De-Schweinitz despite an interim reversion to Nuttall as the author by Gray in 1874. It is probably from the first two citations that Rydberg perpetuated the error in author citation that Torrey and Gray propagated. The new combination published by Rydberg in the *North American Flora* (1915), despite the erroneous author citation, is the legitimate name for this taxon. It should be emended so as to have reference to the correct author and nomenclatural type and is to be written as follows: *Helenium pinnatifidum* (Nutt.) Rydb.

The binomial *Helenium vernale* Nutt. ex A. Gray (Proc. Am. Acad. Arts & Sci. **9**: 204. 1874) is probably a bibliographic error on the part of Gray who misattributed the epithet to Nuttall instead of correctly so to Walter. Rydberg, in dealing with the synonymy of this taxon, seems to have interpreted this error of Gray's as being Gray's intention to publish the binomial *H. vernale* A. Gray. In indicating this supposed homonymy Rydberg cites *H. vernale* Watt. (N. A. Fl. **34** (2): 130. 1915) as the prior homonym. In itself, the "Watt." is inaccurate as to authority, though it probably represents a typographical error. In either case, both of the Rydbergian references (*H. vernale* Gray and *H. vernale* Watt.) have no status under Article 37, in that they are not validly published, being merely cited as synonyms.

Early in the last century James MacBride provided Stephan Elliott with an adequate basis⁴ for separating this species from *Helenium vernale* Walt., the taxon with which it is most often confused. *Helenium pinnatifidum* (Nutt.) Rydb. may be distinguished from *H. vernale* Walt. by the following characters:

1. Mid-cauline leaves barely decurrent, the wing being rapidly tapered and 5 mm. or less in extension along the stem

⁴ In a letter now mounted with the lectotype of *Leptopoda puberula* MacB. in Ell., MacBride provided Stephan Elliott not only with epithets but with descriptions as well of two taxa which Elliott used practically *verbatim* for *Leptopoda puberula* and *L. decurrens* in his *Sketch of the Botany of South Carolina and Georgia*. For this reason, these binomials are attributed here to MacBride with Elliott as the author of the work in which they were published (cf. Article 46, recommendation 46B, 1956 ed., Int. Code Bot. Nom.)

2. The achenes are pubescent, usually very markedly so, with long rufous hairs

3. The peduncle is pubescent, especially in that portion immediately below the involucre proper

4. The radical leaves are not petioloid.

Subsequent to MacBride and Elliott, Nuttall described the species, *Leptopoda pinnatifida*. This differed from *L. puberula* (which Nuttall did not recognize) primarily on the basis of "radical and lower leaves incisely pinnatifid, with remote segments" as opposed to the "slightly repand, with an occasional serrature" of Macbride's *L. puberula*. Beginning with Torrey & Gray, who treated *L. pinnatifida* as a variety only of *L. puberula*, a realignment of *L. pinnatifida* was started. This realignment ended with Gray's treatment of both *L. puberula* and *L. pinnatifida* as synonyms (though misapplied) of *Helenium vernale*. Rydberg in his treatment of 1915, however, recognized both of the leaf forms as being specifically distinct, one as the misapplied *H. vernale* and the other as *H. pinnatifidum*.

In the course of this revision no other morphological character could be found that had a correlation with the pinnatifid leaf, nor could any habitat preference or geographical correlation be made. In the absence of any such correlation, the pinnatifid-leaved plants are here recognized as being the same taxon as *Leptopoda puberula* and are treated as such, although the epithet *pinnatifidum* must, perforce, be used. As particular corroborative data, Figure 8 is presented. It presents ideo-diagrams of the basal leaves from selected plants of a mass collection made by Dr. R. K. Godfrey (*Godfrey 53147*, undistributed) in a single locality of Franklin County, Florida. The upper row represents leaves from plants grown in the Duke University greenhouses while the lower two rows represent leaves from pressed plants (soaked 12 hours so as to approach the living condition) collected in the field. The persistence of variation in the leaf margin of these plants of the same colony which were grown in the greenhouse would indicate that the margin variation is related to some genetic factor(s), whereas the extreme variation within the field-collected plants would indicate that the final expression of this margin character is mediated to a large extent by environmental conditions and probably on a very micro-habitat basis.



FIGURE 8. Ideodiagrams of the basal leaves of *Helenium pinnatifidum* (Godfrey 53107, Franklin Co., Fla.) Row A. Leaves from plants grown under greenhouse conditions. Row B-C. Leaves from plants as they were collected in the field.

Amongst all the specimens of *Helenium pinnatifidum* examined, only three could be considered as possessing glabrous achenes. Torrey and Gray, on the basis of a specimen of *H. pinnatifidum* collected in Georgia by LeConte which had glabrous achenes, published the species *Leptopoda incisa*. This binomial has been appearing off and on in the literature as a recognized taxon at various levels. The first of the three specimens referred to above (*Moldenke 392a*, Broward Co., Fla. DUKE) has achenes whose surfaces are warty, rather than truly glabrous. The duplicates of this collection (MO, NY, PENN) however, have achenes that are of the usual hairy-pubescent kind found in this species. The second specimen (*Ledin s. n.*, 20 Feb. 1947, Dade Co., Fla. FLAS) has achenes that are entirely glabrous. The third specimen, the type of *L. incisa*, has glabrous achenes but a probable duplicate of this collection by LeConte (PH) has the usual hairy-pubescent achenes, unlike the glabrous ones of the type. Otherwise, these three specimens agree with the others of *H. pinnatifidum*. In this treatment, on the basis of such a sporadic occurrence and extremely low frequency, no formal taxonomic recognition is given to those rare specimens of *H. pinnatifidum* that possess glabrous achenes.

The pappus scales of *Helenium pinnatifidum* provide no reliable means for distinguishing between it and *H. vernale*. The pappus scales of both are similar and exhibit the same patterns of variation. However, the similarities can be taken to confirm the closeness of relationship between these two taxa.

The break in the distribution of this species into two segments, one centering on Florida and the other on the Carolinas, is vivid enough to have stimulated a close analysis. Despite a close scrutiny of the specimens no significant geographical correlations with morphological features could be observed. Whether the absence of specimens from the South Carolina-Georgia Coastal Plain areas is a real absence or is the result of absence of collecting in that area, it is impossible to state. However, the author made a specific trip through the counties of Florence, Berkeley, Williamsburg, Dorchester, northern half of Charleston, Georgetown, Horry, Marion and Dillon of South Carolina in the spring of 1955 particularly searching for plants of this species. The results of this search were negative.

(To be continued)